

Research



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A latitudinal gradient in thermal transgenerational plasticity and a test of theory

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Transgenerational plasticity (TGP) occurs when phenotypes are shaped by the environment in both the current and preceding generations. Transgenerational responses to rainfall, CO₂ and temperature suggest that TGP may play an important role in how species cope with climate change. However, little is known about how TGP will evolve as climate change continues. Here, we provide a quantitative test of the hypothesis that the predictability of the environment influences the magnitude of the transgenerational response. To do so, we take advantage of the latitudinal decrease in the predictability of temperatures in near shore waters along the US East Coast. Using sheepshead minnows (*Cyprinodon variegatus*) from South Carolina, Maryland, and Connecticut, we found the first evidence for a latitudinal gradient in thermal TGP. Moreover, the degree of TGP in these populations depends linearly on the decorrelation time for temperature, providing support for the hypothesis that thermal predictability drives the evolution of these traits.

1. Introduction

Long-term trends in global temperature pose clear and well-documented threats to biodiversity [1,2]. Predicting how species will respond is critical to designing robust conservation and management plans. To date, most research attention has focused on shifts in species distributions, within-generation phenotypic plasticity and contemporary evolution as the primary mechanisms of response (see e.g. [3]). However, recent results suggest that epigenetic inheritance and transgenerational plasticity (TGP) may also play important roles in how species cope with changes in climate [4–16]. TGP occurs when phenotypic responses to environmental variables are shaped, in part, by the environment in preceding generations—in the absence of DNA sequence changes. Although definitions vary widely, in our usage, TGP is manifest as a significant interaction between parent and offspring environments affecting offspring phenotype and, as such, generalizes well-studied maternal effects [17,18].

Transgenerational responses to climate-relevant variables such as rainfall, CO₂ and temperature have been observed across the tree of life [5,15]. However, it is currently unclear how the capacity for TGP will evolve as climate change continues. Indeed, there is the considerable current debate over whether epigenetic phenomena are actually relevant to evolution [19–21]. Although theory

predicts a range of potential responses (e.g. [22–25]), these disparate models all concur that the degree to which the parent's environment predicts that of the offspring is critical in shaping the evolution of TGP. Transgenerational responses to predation in *Daphnia* provide qualitative support for this prediction [26] as does a laboratory study on sticklebacks [8]. In this paper, we quantitatively test a key theoretical prediction: that the predictability of the environment influences the magnitude of the transgenerational response. Since environmental predictability is likely to shift with climate change [27,28], this comparison is critical to predicting species responses.

Here, we take advantage of a naturally occurring gradient in predictability to test this theory. The Atlantic coast of the US exhibits one of the steepest latitudinal gradients in seasonality in the world [29]. Somewhat less well-known, there is also a latitudinal gradient in thermal predictability within a growing season (electronic supplementary material, figure S1): the autocorrelation in temperature drops off most rapidly at high latitudes. In the light of this, the available theory predicts that local adaptation in TGP in response to temperature on the US East Coast, if it exists, should decrease with increasing latitude.

To test this hypothesis, we used the sheephead minnow (*Cyprinodon variegatus*) as our model system. Sheephead minnows are small estuarine fish found in shallow waters on the US east coast from MA to FL. Salinas & Munch [4] showed that sheephead minnows from Florida exhibit thermal TGP such that the fastest growing offspring at a given temperature are those whose parents were held at the same temperature. To test whether a latitudinal gradient in thermal TGP exists, we quantified thermal TGP in growth and maturation in sheephead minnows from South Carolina (SC), Maryland (MD), and Connecticut (CT).

2. Methods

Several hundred wild sheephead minnows were collected from tidal ponds in SC, MD and CT and transported to the wet laboratory at the Southwest Fisheries Science Center in Santa Cruz, CA. Location data are provided in the electronic supplementary material, table S1. Fish were held in the laboratory at 24°C for at least two months prior to the start of the experiment. Throughout the experiment, all fish were maintained in 120 l sea tables with filtered recirculating water at 21 ppt salinity, 14 L:10 D photoperiod, and provided unrestricted food.

At the start of experiment 30 randomly selected breeding pairs from each population were acclimated over one week to either 26°C or 32°C and thereafter maintained at these temperatures for up to 45 days. Eggs were collected from each pair after 7, 30 and 45 days of exposure to treatment temperatures. Egg collections were completed within 4 h of fertilization to minimize exposure to the parents' environment. Each clutch was immediately subdivided into two groups and transferred to 26°C and 32°C. When the fish were approximately 4 mm on average, up to five larvae from each half-clutch were transferred to individual rearing containers. Three sea tables per temperature each housed approximately 30 individuals from each population. Overall numbers for each population and temperature are given in the electronic supplementary material, table S1. The individual length was measured weekly using digital photography (Canon EOS 40D with 18–55 mm lens). Male sheephead minnows go through a predictable sequence of four colour stages as they approach maturity that is closely tied to investment in gonad development [30]. Each week, colour stage was recorded for all male offspring.

To obtain a continuous estimate of maturation age, we linearly interpolated the colour stage time series for each individual.

For each population and egg collection (i.e. the 7-, 30-, and 45-day parent temperature treatment intervals), we tested for the presence of TGP in growth and maturation. To facilitate comparison with previous experiments [4], temperatures were scaled by the difference between the experimental mean (T_{avg}) and pre-trial acclimation (T_{acc}) temperatures, i.e. $T_{\text{scaled}} = (T - T_{\text{avg}}) / (T_{\text{avg}} - T_{\text{acc}})$, specifically $T_{\text{avg}} = 29^\circ\text{C}$ and $T_{\text{acc}} = 24^\circ\text{C}$ here and $T_{\text{avg}} = 29^\circ\text{C}$ and $T_{\text{acc}} = 21^\circ\text{C}$ for Salinas & Munch [4]. For consistency with our earlier work, we determined juvenile growth rate (mm d^{-1}) from the change in size over the first eight weeks for all fish. Time to maturation (males only) was analysed in the same way, but with individual growth rate included as an additional covariate.

All analyses used linear mixed-effect models with family ID as a random effect and were performed in R using lme4. First, we fit a model including offspring temperature, parent temperature and their interaction along with parent lengths and egg diameter as covariates (e.g. $\text{growth} \sim T_{\text{par}} * T_{\text{off}} + D_{\text{egg}} + L_{\text{sire}} + L_{\text{dam}} + (1 | \text{family})$), where T_{par} is the parent temperature, T_{off} is the offspring temperature, D_{egg} is the egg diameter, L_{sire} is sire length, L_{dam} is dam length and $(1 | \text{family})$ is the random intercept for family). Including an additional random effect for offspring temperature (i.e. a family-level reaction norm) did not change any of the results for the fixed effects for growth. For maturation, where the sample sizes are much smaller, models with this additional random effect did not converge. We therefore report results for the random intercept model only.

Because our main interest is in the interaction between parent and offspring temperature, effects of egg diameter and parent size are nuisance covariates. Likelihood ratio tests indicated that these nuisance covariates did not contribute significantly. Hence, subsequent evaluations of the temperature effects for each population and treatment were carried out on the reduced model, $\text{growth} \sim T_{\text{par}} * T_{\text{off}} + (1 | \text{family})$ using type III SS with Satterthwaite's method to approximate the degrees of freedom, implemented in the R package lmerTest.

The experimental results were combined with field temperature records for each population to quantitatively assess how the degree of TGP varies with the predictability of the environment. We used the first-order interaction of parent and offspring temperature on growth rate and maturation time to quantify the degree of TGP. To compare the degree of TGP with the predictability of the environment, temperature data for each region were obtained from nearby sites in the National Estuarine Research Reserve (see electronic supplementary material, table S2). Using data from 2008 to 2015, we determined the growing season in each location as the time interval over which the mean temperature exceeded 21°C and estimated autocorrelation functions for each site. We calculated the decorrelation time, t_0 , as the first zero of the pooled ACF for each region. The decorrelation time measures the period over which the current temperature is positively correlated with future temperatures. In the context of TGP, the decorrelation time provides an upper bound on the length of the time interval through which the offspring environment can be predicted by the parental environment. We use the decorrelation time as our index of thermal predictability, though other indices are certainly possible [31].

To test the hypothesis that the degree of TGP depends on the predictability of temperature, we re-analysed the experimental data for SC, MD and CT combined using three models for differences among populations. Model 1 allowed unconstrained differences among populations in their response to temperature. Specifically, we fit $\text{growth} \sim T_{\text{par}} * T_{\text{off}} * \text{Pop} + (1 | \text{family})$ with the factor 'Pop' indicating population. Model 2 constrained differences among populations to be proportional to the decorrelation time (i.e. the continuous variable decorrelation time replaced the

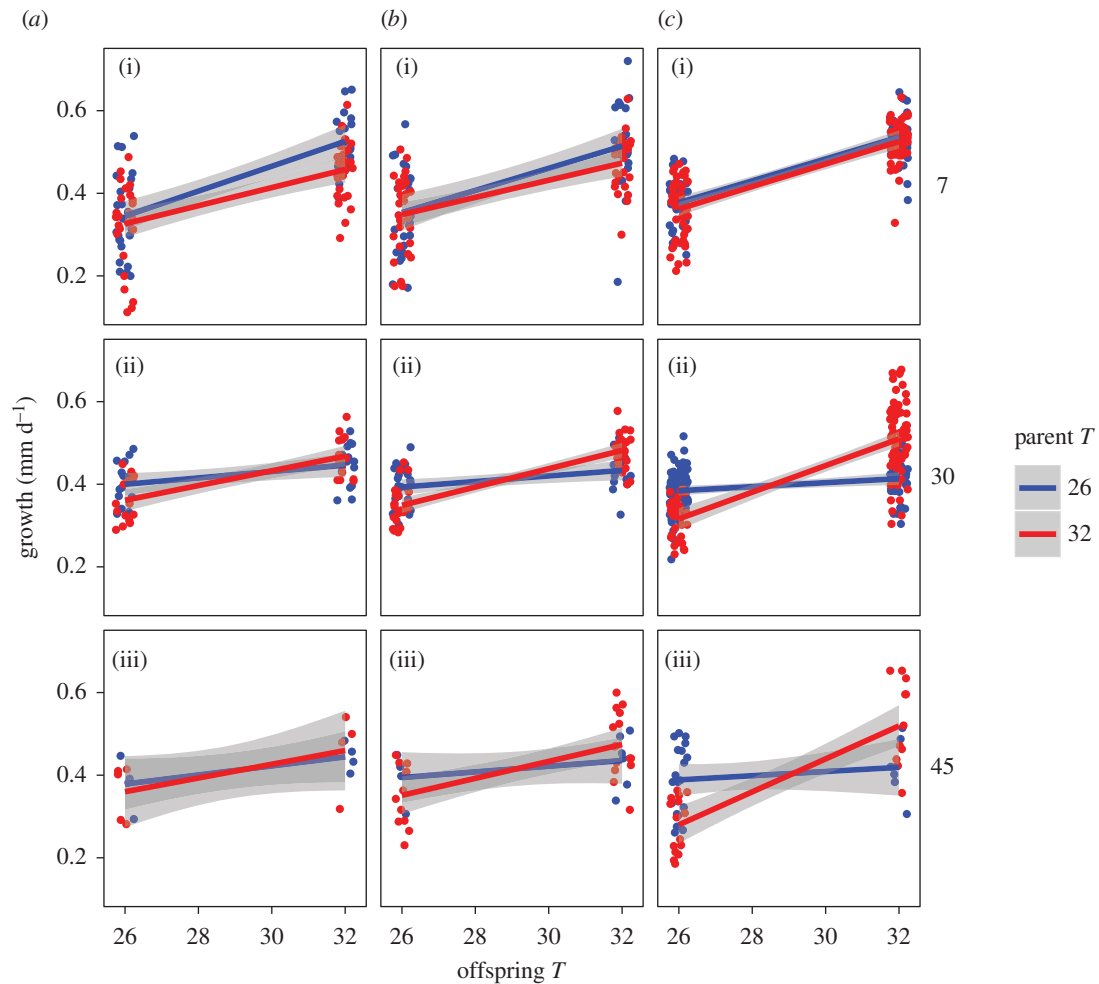


Figure 1. Growth versus temperature for each population and parent temperature exposure time. Within each plot, the horizontal axis is the temperature at which the offspring were reared and the vertical axis is the growth rate over the first eight weeks in mm d^{-1} . The points are results for individual fish, with blue and red indicating that their parents were at 26 and 32°C, respectively. The lines are least-squares regressions fit separately for each parent temperature and are intended as a visual aid, rather than a formal analysis. Columns indicate results for fish from CT, MD and SC, (a), (b) and (c), respectively; the rows (i–iii) indicate results for the 7-, 30- and 45-day exposure treatments. (Online version in colour.)

factor population, using $\text{growth} \sim T_{\text{par}} * T_{\text{off}} * t_0 + (1 | \text{family})$. Model 3 treated all populations as identical (i.e. $\text{growth} \sim T_{\text{par}} * T_{\text{off}} + (1 | \text{family})$). Comparing models 1 and 3 tests whether there were any significant differences among populations. Comparing models 1 and 2 explores whether the population effect can be adequately explained by the decorrelation time. As an independent test of the effect of decorrelation time, we then used model 2 to extrapolate the degree of TGP in growth for fish from FL and compared the result to previously collected data from Salinas & Munch [4].

3. Results

(a) Existence of transgenerational plasticity along the US East Coast

Egg diameter and parent length did not contribute significantly to variation in growth (electronic supplementary material, table S3). Offspring growth increased significantly with offspring temperature for fish from all populations (figure 1; electronic supplementary material, table S4). Among offspring from the 7-day parent exposure, there were no significant effects of parent temperature and no significant interactions between parent and offspring temperatures. That

is, after the parents spent 7 days at their new temperatures, no population exhibited TGP.

After 30 days of temperature exposure, however, offspring growth in all three populations exhibited a significant interaction between parent and offspring temperature (SC: interaction (s.e.) = 0.11 (0.012), $p < 0.001$; MD: 0.06 (0.014), $p < 0.001$; CT: 0.04 (0.018), $p = 0.02$), demonstrating a shift in reaction norms of offspring resulting from temperature experienced by their parents (see electronic supplementary material, table S4 for further details). Offspring from high (32°C) and low (26°C) temperature parents grew at rates that differed by as much as 23.2% (0.31 versus 0.25 mm d^{-1} at 32°C for fish from SC) though the magnitude of this effect appears to decrease with latitude (figure 1d–f; electronic supplementary material, table S4).

After 45 days of exposure, there were substantial differences in TGP among populations. The offspring growth rate in SC remained significantly affected by the interaction of parent and offspring temperatures (interaction (s.e.) = 0.15 (0.035), $p < 0.001$), while fish from MD and CT exhibited reduced, non-significant transgenerational effects (figure 1g–i; electronic supplementary material, table S4). However, relatively few families produced offspring for this egg collection (electronic supplementary material, table S3) and the lack of significance may be due to the relatively small sample sizes. The difference

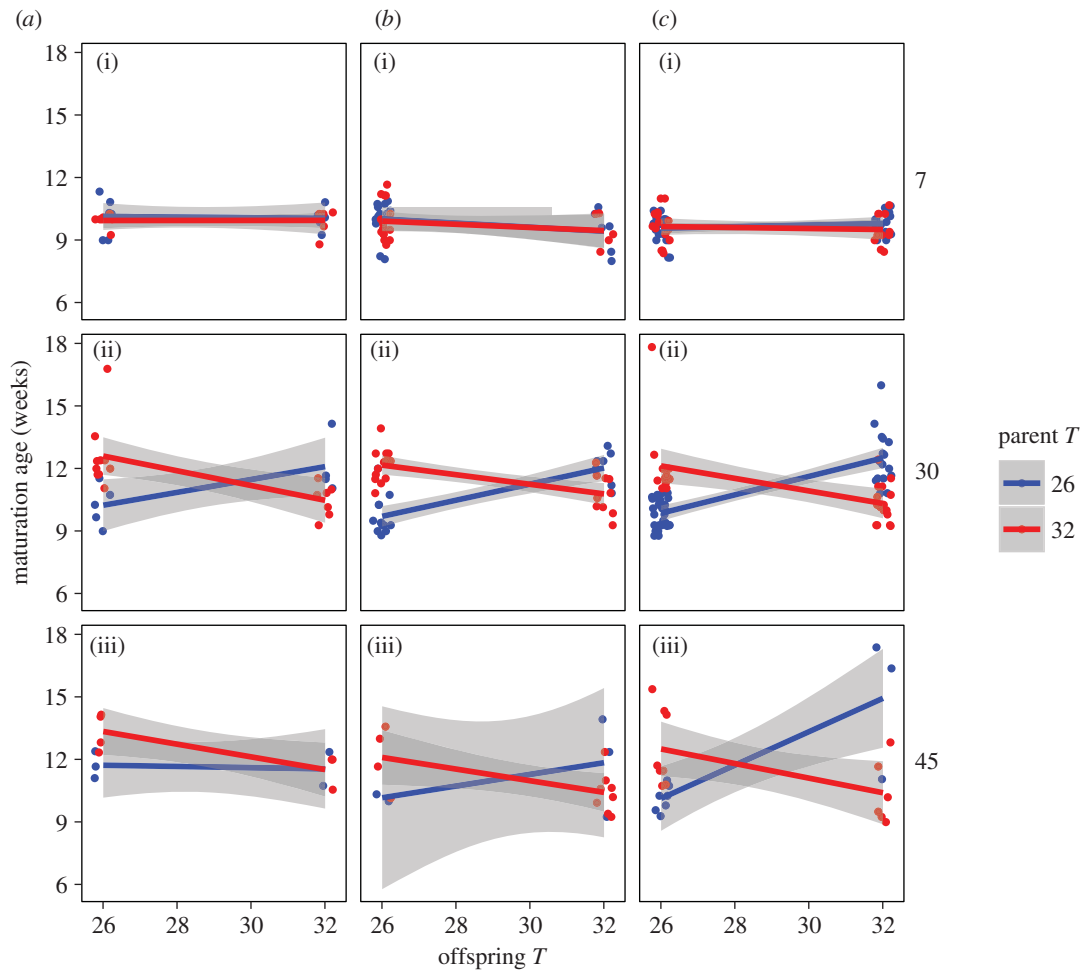


Figure 2. Maturation versus temperature for each population and parent temperature exposure time. Within each plot, the horizontal axis is the temperature at which the offspring were reared and the vertical axis is the interpolated maturation age in weeks. The points are results for individual fish, with blue and red indicating that their parents were at 26 and 32°C, respectively. The lines are least-squares regressions fit separately for each parent temperature and are intended as a visual aid, rather than a formal analysis. Columns indicate results for fish from CT, MD and SC, (a), (b) and (c), respectively; the rows (i–iii) indicate results for the 7-, 30- and 45-day exposure treatments. (Online version in colour.)

among populations in the effective duration of TGP is discussed further below.

Age at maturation also exhibited a strong degree of TGP, depending on the duration of parental exposure (figure 2; electronic supplementary material, tables S5 and S6) and was largely independent of egg diameter, parent length and offspring growth (electronic supplementary material, table S5). After 7 days of exposure, there were no effects of parent or offspring temperature. After 30 days, however, there was a significant interaction between parent and offspring temperature in all populations (SC: interaction (s.e.) = -2.90 (0.39), $p < 0.001$; MD: -2.58 (0.34), $p < 0.001$; CT: -2.76 (0.74), $p = 0.001$). See electronic supplementary material, table S6 for further details. After 45 days of exposure, the interaction between parent and offspring temperature remained significant for fish from SC (interaction (s.e.) = -4.80 (1.055), $p < 0.001$) and MD (-2.33 (1.06), $p = 0.047$), but not in CT (-1.12 (0.719), $p = 0.16$).

We used the parent temperature \times offspring temperature interaction term to quantify the degree of TGP. Doing so, we found that the degree of TGP depends on the parental temperature exposure time in a pattern that appears to change with latitude for both growth (figure 3a) and maturation (figure 3b).

(b) Latitudinal gradient in transgenerational plasticity and environmental predictability

To test the hypotheses that the observed latitudinal gradient in the degree of TGP depends on the predictability of the environment (as in figure 3), we compared the fit of three models where (i) population differences are unconstrained, (ii) the effect of population is linear in the decorrelation time and (iii) there are no differences among populations.

Comparing models 1 and 3 for growth indicates that there are significant differences among populations after the 7- and 30-day parent exposures (electronic supplementary material, table S7). Population differences were no longer significant at the 45-day exposure, though this may be due to the relatively small numbers of offspring produced during this egg collection. Comparing models 1 and 2 indicates that the differences in TGP among populations are well explained by the differences in decorrelation time (all $p > 0.88$). In addition, model 2 was significantly better than model 3 indicating that the differences among populations are adequately modelled as a linear function of the decorrelation time. In each case, the degree of TGP in growth increases with the decorrelation time (figure 4). Importantly, further support for the relationship between environmental predictability and the degree of TGP (figure 4) comes from extrapolating

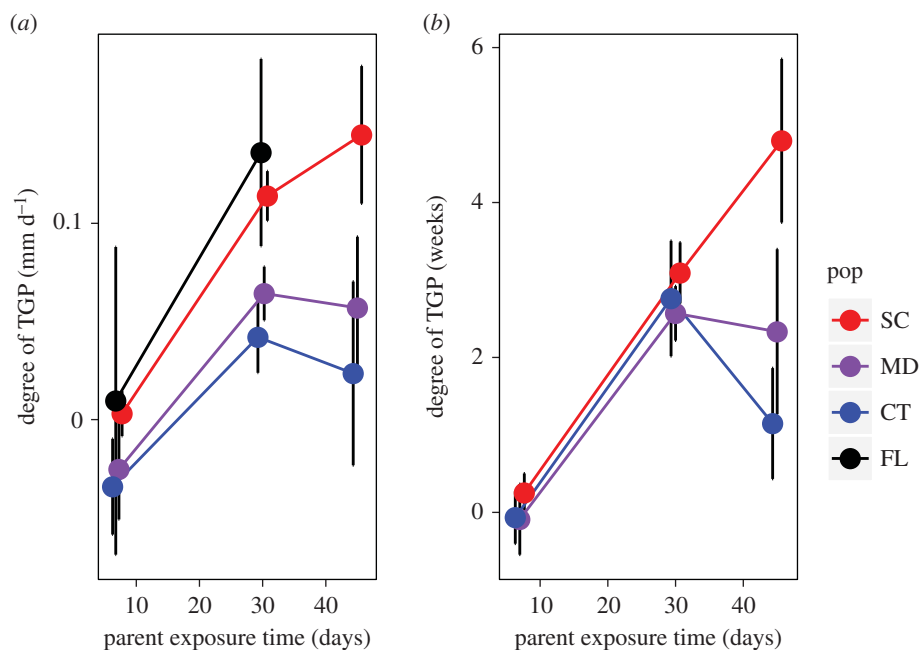


Figure 3. Population differences in the degree of TGP. In each panel, the horizontal axis is the duration of the parent temperature exposure (days) while the vertical axis is the degree of TGP, measured as the interaction between parent temperature and offspring temperature for (a) growth and (b) maturation. (Online version in colour.)

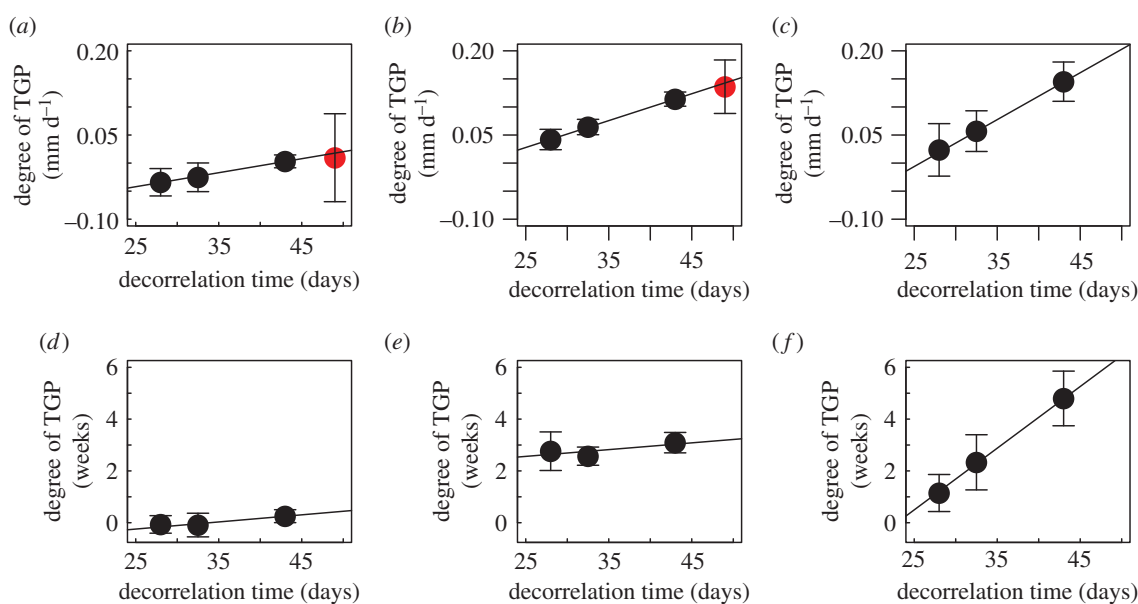


Figure 4. Degree of TGP versus decorrelation time for each parent exposure time. Within each plot, the horizontal axis is the decorrelation time and the vertical axis is the degree of TGP and black points are estimates from each of the population and exposure time-specific analyses. The black line is the estimate of the relationship between the degree of TGP and the decorrelation time fitted to the data for each exposure time with all populations combined; (a), (b) and (c) are for growth rate; (d), (e) and (f) are for maturation time, and from left to right the columns correspond to the 7-, 30-, and 45-day exposure times. The red points in panels (a) and (b) are independent estimates for fish from FL (previously published in [4]) that were not used in fitting the model. (Online version in colour.)

this model using the decorrelation time for Florida. The predictions for both the 7- and 30-day exposures closely match the degree of TGP reported previously [4].

By contrast, for maturation, populations differ significantly only at 45 days (electronic supplementary material, table S8). The comparison of models 1 and 2 indicates that population differences in the degree of TGP in the 45-day exposure is linear in the decorrelation time. However, although consistent with our results for growth rate, we note that there were relatively few maturing males from the 45-day exposure, particularly from northern populations.

4. Discussion

There is now a substantial body of theory on the evolution of TGP spanning several decades (e.g. [22–25]). Although some models make more nuanced predictions than others, all agree that the fitness benefits of TGP depend on how much information the parents' environment can provide about the environment their offspring are likely to face. Based on this, we hypothesized the existence of a previously unobserved latitudinal gradient in TGP. The concordance between the decorrelation time for estuarine temperatures and the

degree of TGP provides quantitative support for this theory in natural populations. Moreover, the earlier data for fish from Florida [4] that were not used in model-fitting provide independent validation of this relationship.

Studies of TGP have recently been criticized as lacking sufficient control for selection and early developmental effects [32]. We note that there was very little adult mortality that occurred between the 7- and 30-day parent exposures (for SC, MD and CT parent survival was 95%, 100% and 70%) strongly limiting the possibility for selective mortality in the parent generation. In addition, the offspring were handled the same way for each egg collection so that differences between the 7- and 30-day egg collections cannot be explained by inadvertent selection on eggs and larvae. We are therefore reasonably confident in attributing the changes in offspring growth to the thermal histories of the parents rather than selective mortality.

Moreover, the response to the parental temperature cue appears to be tied to the seasonal thermal regime for each population. Considering that the degree of TGP in growth changes with parent exposure time in a manner that appears approximately parabolic in each population (figure 3), fitting a quadratic model to these estimates allows us to determine (i) the exposure time required to express the maximum degree of TGP and (ii) the duration of TGP (i.e. the period of time over which the degree of TGP is expected to be greater than 0). Doing so, we find that both the timing/duration of TGP decreases with latitude from 53/93 days in SC to 43/63 days and 40/54 days in MD and CT, respectively. Based on the NERRS temperature data, the duration of the growing season also decreases sharply with latitude (see electronic supplementary material, figure S1). The number of days for which the mean temperature was at or above 21°C was 209, 184, 116 and 103 for FL, SC, MD and CT, respectively. Although strictly exploratory, the timing and duration of TGP estimated this way strongly correlated to the duration of the growing season, $r=0.998$ and 0.999 , respectively (figure 5). From this, we hypothesize that both environmental predictability and season duration jointly drive the evolution of TGP, particularly in environments where seasonal variation in the growth of juveniles is an important determinant of fitness.

Although this has not yet been the subject of theoretical investigation, the correlation between the duration of the growing season and the apparent duration of TGP is intuitively reasonable: the fitness benefits of programming offspring for maximal growth at a future temperature must depend critically on the local environmental regime. In addition, we should expect the marginal gain from rapid growth to decrease as parents approach the end of the growing season. Mortality during the early life history of fishes is strong size selective [33], suggesting that the observed pattern of TGP is adaptive. However, there are clearly contexts where rapid growth is not optimal (e.g. [34]). In fact, many species on the US East Coast exhibit countergradient variation in growth (Conover and Present REF), such that populations from higher latitudes grow faster than low latitude conspecifics at a common temperature. In this light, it is interesting to note that sheepshead minnows did not display an obvious latitudinal gradient in growth rate. Clearly, more information is needed to determine the optimal growth and maturation schedule for sheepshead minnows from different latitudes. Nevertheless, this connection between seasonality and TGP

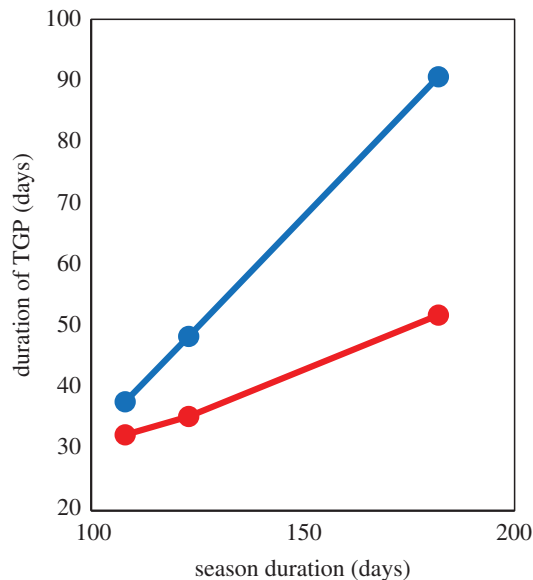


Figure 5. Timing of TGP versus growing season duration. The horizontal axis is the duration of the growing season estimated as the number of days for which the mean temperature was greater than or equal to 21°C, averaged across the two NERRS sites for each state. The red line indicates the estimated time at which the degree of TGP is maximized. The blue line indicates the duration of TGP, defined as the period of time over which TGP is non-zero. Each was estimated from a quadratic fit to the degree of TGP in growth for each population provided in figure 3 for each population (except FL). (Online version in colour.)

highlights the need for a more nuanced theory that incorporates seasonal environmental variation within generations (but see [25]).

In addition, these results shed light on an apparent paradox in the literature on transgenerational effects. Salinas *et al.* [5] found that evidence for TGP is distributed across the tree of life, while a contemporaneous meta-analysis by Uller *et al.* [35] concluded that typical effect sizes are close to 0. One resolution to this discrepancy is that the timing and environmental conditions under which TGP is expressed may be quite specific and vary considerably among populations. For instance, had we only measured TGP after a 7-day exposure to different temperatures, we could only have concluded that TGP does not exist. In the light of these results, we propose that TGP is most likely to be relevant over relatively brief intervals during which survival of offspring can be substantially enhanced by modified reaction norms. Experiments investigating the existence of TGP must therefore be carefully designed to reflect the temporal patterns of environmental variability experienced by the population being examined.

The existence of a latitudinal gradient in TGP has important implications for how species will respond to climate change. On the one hand, we know that many species can exhibit TGP, which means that the capacity for rapid, non-genetic responses to shifts in climate is widespread. On the other hand, global climate model predictions indicate that the greatest changes in climate will occur at higher latitudes (e.g. [36]). If latitudinal gradients in thermal TGP occur in other species—as predicted implicitly by theory and demonstrated here for sheepshead minnows—then the capacity for TGP is likely to be weakest where climate change will be most severe. While we were previously sanguine about TGP as a mechanism for coping with climate change [4,5], we now suspect that the rate at which TGP can evolve to

match the environment will be critical in determining its utility for buffering populations against climate change.

Ethics. All work was approved by the relevant entities.

Data accessibility. The dataset and code are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.18931zcx6> [37].

Authors' contributions. S.B.M.: conceptualization, formal analysis, funding acquisition, project administration, writing-original draft, writing-review and editing; W.L.: conceptualization, formal analysis, investigation, writing-review and editing; M.W.: writing-review and editing; T.H.: writing-review and editing; B.A.W.: investigation, writing-review and editing; M.M.: funding acquisition, writing-review and editing; S.S.: conceptualization, writing-review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Competing interests. We declare we have no competing interests.

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